The following article is translated by David Heaf from the original German article *Natürliche Zellgröße* by Eric Zeissloff which appeared in the *Journal Apicole Luxembourgeois* (March, 2007). Although it would be normal to translate the French or German terms for the old Parisian units of measurement *pied du roi/Fuß*, *pouce/Zoll* and *ligne/Linie* into *foot*, *inch* and *line*, Zeissloff's article also mentions the Imperial units of that name. Thus, in order to preserve the distinction throughout, the author's German terms have been retained.

Parisian unit	Metric (cm)		English term	Imperial size (approx.)
Pied du roi / Fuß	32.483	= 12 pouces	foot	1 ft. 25/32 in.
Pouce / Zoll	2.7069	= 12 lignes	inch	1 1/16 in.
Ligne / Linie	0.2256		line	3/32 in.

Natural cell-size

Eric Zeissloff

In the last ten years the hypothesised has arisen that the cell-size (circa 5.4-5.5 mm diameter) of foundation on sale no longer corresponds to the natural size of honey bee comb cells. Small cells have been associated with a resistance to Varroa, and under certain conditions this is also the case or appears to be. Whether or not small cells favour Varroa resistance is not the subject of this article. Here we are concerned only with establishing what cell size the bees build under natural conditions.

In order to do this we have some published sources available. These sources are of two kinds: those which came before the use of foundation and those which came after it was introduced. Furthermore, these sources need to be tested for reliability.

The following authors are mentioned:

Maraldi, Giacomo Filippo (1665-1729) Réaumur, René Antoine Ferchault de (1683-1757) Castillon, Christ, Johann Ludwig (1739-1813) Lombard, Charles-Pierre (1743-1824) Lhuillier, Simon-Antoine (1750-1840) Féburier, Charles Romain Dzierzon, Johannes (1811 - 1906) Berlepsch, August Freiherr von (1815 - 1877) Cowan, T. (1840-1926) Ludwig, August (1867-1951) Baudoux, Ursmar (1867-1934) De Meyer, Etienne (1892-1967)

De Meyer

In his book *Guide practique apicole* (Practical guide to beekeeping) De Meyer wrote about the experiments of Badoux: "In nature we can count 850 cells (on both sides) per dm². Nowadays foundation of 850, 800, 750 and 640 cells/dm² is available commercially. In Belgium, foundation of 850 and 800 cells has practically disappeared."

On drones he wrote the following: "Colonies with 850 cells/dm² build 527 drone cells per dm². Badoux showed that the bigger the bees the bigger the drones and always in the same proportionality. It can happen that the queen lays drone eggs in 640-cell and the drones that emerge from it are too small and an imbalance arises."

According to the table published by Badoux, 850 cells/dm² corresponds to a diameter of 5.21 mm and 527 cells/dm² to a diameter of 6.6 mm.

Ludwig

In his book *Unsere Biene* (Bees), published in 1906, Ludwig wrote about comb construction: "If we measure the thickness of finished comb it is usually 22 to 24 mm. In a strong nectar flow, however, honey cells are lengthened, which results in the greater thickness of such comb" [...] "On average 1 dm² of comb contains 850 worker or 510 drone cells on both sides."

510 cells/dm² corresponds to a diameter of 6.73 mm.

Cowan

The following is taken from Cowan's *The honey bee: Its natural history, anatomy and physiology* (1890) [Translating back from German, *Tr.*]:

Worker cells measure 1/5th inch from one parallel side to the one opposite and 13/64^{ths} inch from one corner to the corner opposite. Correspondingly, drone cells are ½ and 9/32 inch.

In a square inch there are 27.5 worker or 17.09 drone cells. Averaged over a larger area there are no more than 25 worker or 16 drone cells to a square inch.

The thickness of a worker bee brood comb is about 7/8^{ths} inch, and that of drone comb 1 ½ inch.

The average diameter of a worker cell is 1/5 inch. Average, because there are significant differences at different points in the same comb.

In addition, if 36 rows of 10 worker cells are measured, the maximum for a row is 2.11 inches and the minimum 1.86 inches.

Further measurements with 60 cells in a row were carried out.

A row 2 inches from the upper edge of the comb measured 12.10 inches.

A row 4 inches from the upper edge of the comb measured 12.00 inches.

A row 2 inches further down measured 12.01 inches.

If 10 cells are measured at the end of this row of 60 and in the middle, there are significant differences.

In the first row: at one end 2.07; in the middle 1.98; at the other end 2.08.

For the second row: 2.1, 1.95, 1.98 For the third row: 2.00; 1.95; 2.05.

These measurements were made on dark bees. Carnica bees showed similar variations. On average the Carnica cells were somewhat larger.

Féburier

In his book *Traité complet théorique et practique sur les abeilles* (Comprehensive treatise on bees: theory and practice), published 1810, Féburier wrote: "...the bees are about 15 mm (6 *Linien*) long and have a diameter of 5 mm (2 linien)."

"The depth of worker cells is usually 12.5 mm (5 *Linien*), the diameter 6 mm (2.4 *Linien*). The depth of drone cells 16 to 17 mm (6.5 to 7 *Linien*), the diameter 8.75 mm (3.5 *Linien*). The queen cell is 3 cm (1 *Zoll*) long, has an inside diameter of 8 mm (3.5 *Linien*), the walls are 3 mm (1.5 *Linien*) thick...".

Berlepsch

The book *Die Biene und ihre Zucht auf beweglichem Rahmen* (1st ed. 1860) by Berlepsch is unfortunately not available to me, but he is said to have mentioned a cell diameter of 2.5 *Linien*.

Dzierzon

"As regards the cell width, there are two kinds. Those in which the worker bees are raised, and which are therefore called bee cells, are narrower, such that 5 of them side by side take up one Zoll; the others, fewer in number, in which the drones are raised, are wider, such that 4 fit into 1 Zoll. But the cells of both kinds are all exactly alike. The width can also be measured in larger spans, for example 2 $Fu\beta$ in length and longer like slabs on which the cells lie beside each other in completely straight lines in three different directions; a single cell always resulting in the same width or breadth. Thus they could be used as a unit of measure that is precisely understood universally, i.e. in any country at any time. At least authors of bee books should refer

the measurements they give and those they use to the cell width. So that my readers can understand the measurement I use and be able to compare it with their own, I state that precisely 5 bee cells go into one Zoll, and 60 into 12 Zoll or 1 $Fu\beta$. It is incredible how the bees are able to build such regular cells always with the same size without a ruler or protractor. This would be less incredible if all cells were the same size as the small bee cells. We would then assume that the bees had on their own bodies some sort of scale for building cells. But that they are in a position to build somewhat larger cells that are suited to the bodies of drones, which are frequently not present at the time, and always of the same width, is even more amazing. In contrast, as regards the depth of individual cells, with brood cells it always fixed and always the same; with bee cells it is about half a Zoll, in accordance with the length of the bee's body, and somewhat larger with drone cells. The depth of the cells assigned only to honey, large as well as small cells, for example those placed uppermost and towards the sides in the cool corners of the hive, where there is no brood, is different. The cells, when they are filled with honey, are extended or the sections made so thick that they almost touch each other or reach the walls of the hive allowing only a single bee to crawl between."

Lhuillier

Memoire sur le minimum des alveoles des abeilles et en particulier sur un minimum minimorum relatif à cette matière (Dissertation on the minimum size of bee cells and in particular on the minimum minimorum relative to this matter. 1781).

The sizes are given in Parisian Zoll.

Number of cells	Row length		Radius of the inner circle
	Zoll	Linien	Linien
15	3		1.2
19	3	10	1.21
20	4		1.2
25	4	11	1.18
23	4	8	1.2173893
21	4	1	1.19
27	5	3.5	1.176
46	9		1.173913
16	3	3	1.21875
40	8		1.2

Lombard

In his book *Etat de nos connoissances sur les abeilles au début du XIX siècle* (State of our knowledge about bees at the start of the 19th century. 1805) Lombard wrote: "In a bee colony there are cells whose depth is 3 cm (1 *Zoll*); others 16 mm (8 *Linien*), and yet others 11 mm (5.5 *Linien*). The diameter of some cells is 4.8 mm (2.4 *Linien*), that of others 6.66 mm (3.33 *Linien*)."

In converting *Zoll* to millimetres, Lombard was probably mistaken. For him 1 *Zoll* = 3 cm and 1 *Linie* 2 mm. I do not know of any *Zoll* which is exactly 3 cm, and which is divided into 15 *Linien*!

Castillon

Castillon wrote the foreword of the work of Lhuillier, published in *Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres* (Annals of the Royal Academy of Sciences and Belles-Lettres) in Berlin in 1783.

Christ

Anweisung zur nützlichen und angenehmen Bienenzucht (Guide to profitable and pleasant beekeeping) (1783) "A normal queen bee of average size, which in life is 10 to 11 Parisian Zoll long, measures no more than 7 Linien when she is dead, and is thus only one Linie longer than a dead worker bee, which is 5½ to 6 Linien long, when dead, and at most 7 Linien, when alive and young. For an old or one year worker bee has already become smaller and shrunken."

Réaumur

In the 5th volume of *Mémoire pour servir à l'histoire des Insectes* (Dissertation on insects. 1742) Réaumur writes: "20 small cells in a row measure altogether 4 *Zoll* minus half a *Linie*. If the half *Linie* is ignored the diameter of a cell is 2.4 *Linien*. A piece of comb 15 *Zoll* long and a little more than 10 *Zoll* wide comprises 9000 cells. 10 drone cells in a row altogether measure 2 *Zoll* 9.4 *Linien*. Thus the diameter of a single drone cell is 3 *Linien* and 17/50^{ths}, i.e. about 3 1/3 *Linien*. When I have measured the drone cells in another direction, only 9 cells came to the length of 2 *Zoll* 9.4 *Linien*. This irregularity is also observable with the smaller cells (worker bee cells)."

"The depth of a worker bee cell is 5 1/3 *Linien*, and the comb about 10 *Linien* thick. Drone cells are sometimes 8 *Linien* deep, but there are some that are not so deep. Honey cells can be over 10 *Linien* deep."

Maraldi

In *Observations sur les abeilles* (Studies on bees. 1712) Maraldi writes: "Within a day they have a comb one $Fu\beta$ long and 6 *Zoll* wide, which can hold about 4000 worker cells."

"Each comb is somewhat thinner than one *Zoll* thick, the depth of a cell is then about 5 *Linien*. On different combs of 1 $Fu\beta$ long one can count 60 to 66 cells."

"The larger cells (drone cells) have a diameter of 3 *Linien* and a depth of about 6 *Linien*."

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1 Fu\beta (Parisian) = 32.483 cm = 12 Zoll
1 Zoll (Parisian) = 2.7069 cm = 12 Linien
1 Linie (Parisian) = 2.256 mm
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Analysis

Bee size

Christ and Féburier give information on the length of the bee's body. If we compare the cell size values of Féburier (the values in *Zoll*) with those of Réaumur, we must assume that both of them had used Parisian *Zoll*.

It would also be possible that Féburier copied the measurements in *Zoll* and recalculated in millimeters with a rounded up *Zoll* (1 *Zoll* = 3 cm). How could we otherwise explain the values of Féburier of a cell diameter (6 mm for worker bee cells and 8.75 for drone cells) in millimeters?

From this we can conclude that at that time a worker bee had a body length of 13.54 to a maximum of 15.8 mm. The queen then had a body length of 22.56 to 24.81 mm.

I have not yet tried to measure a bee, but in modern beekeeping literature the following values for body length can be found:

Queen: 16 to 25 mm Worker: 12 to 15 mm

The queen cell then had a length of 27.07 mm and an inside diameter of 7.9 mm.

Cell size

It is remarkable that from Maraldi to Dzierzon the diameter of a worker cell is always about 2.4 *Linien* and that of a drone cell about 3.3 *Linien*. The width of a comb is also always 10 to 11 *Linien* or 22 to 24 mm.

How can this be explained?

I can think of three possibilities:

- 1. All authors have not used as a the basis of their measurements the usual unit of measure of their country or district, but have decided on the Parisian *Zoll*.
- 2. Most authors have copied from Maraldi, Réaumur of Lhuillier.
- 3. The bees have such a high level of consciousness that to build their comb they have been guided by the units of measurement of the country in which they find themselves.

First of all I will immediately reject the third hypothesis. This leaves the first and second.

Maraldi, Réaumur, Lhuillier and Cowan certainly did their own measurements. From this the natural average cell size of a colony would be 2.4 Parisian *Linien* (5.4144 mm) and for Drone cells 3.33 Parisian *Linien* (7.51 mm).

However, the measurements were not carried out in all three directions. As the cells are not perfect hexagons the average values can vary downwards or upwards. This could explain the value of 7.51 mm for a drone cell.

In a colony the cell size varies according to its position on the comb and to the time at which it was constructed.

The measurements were all made on *Apis mellifera mellifera* colonies. Cowan had also apparently carried out measurements on Carnica and Ligustica colonies. In his book he stated that the Carnica bee builds somewhat bigger cells than the dark bee.

As a conclusion we can state that the modern bees are not significantly bigger than during the last 300 years (disregarding the enlargement experiments of Badoux).

Furthermore, in the bee colony, uniformly smaller cells (4.9 or 5.2 mm) are just as unnatural as the larger cells (5.4 or 5.5 mm).

Zeissloff Eric Seestraße 24 13353 Berlin +49 33 45493723 z.eric@onlinehome.de